

1986

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### Recommended Citation

Michener, David C. (1986) "Systematic and Ecological Wood Anatomy of Californian Scrophulariaceae. II. Penstemon Subgenus Saccanthera," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 11: Iss. 3, Article 8.  
Available at: <http://scholarship.claremont.edu/aliso/vol11/iss3/8>

SYSTEMATIC AND ECOLOGICAL WOOD ANATOMY OF CALIFORNIAN  
SCROPHULARIACEAE. II. *PENSTEMON*  
SUBGENUS *SACCANTHERA*

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ABSTRACT

Wood anatomy of nonarboreal Scrophulariaceae is little studied, yet such information is needed to understand the evolution of woodiness in the family and order. Description and quantification of wood characters of six species (nine taxa) of *Penstemon* subgenus *Saccanthera* show that these woods are specialized. Paedomorphic features include the standard declining-to-level curve of vessel element length by age, and (in several samples) a pronounced tendency to raylessness. Variation in ray characteristics is as great within as between species, suggesting that unsampled populational variation in ray characteristics may be present. Cells intermediate between fibers and nonseptate parenchyma are present and complement the biseriate strands of axial parenchyma. Storying of cambia is found in two species. Crystal presence is erratic; when present, crystals are restricted to pith and rays. Interpreting the paedomorphic origin of the woody habit in *Penstemon* as an example of heterochrony suggests that comparative life-history and resource-allocation studies may provide powerful tools for placing woodiness in an ecological and evolutionary context in this complex genus.

Key words: ecology, *Penstemon*, *Saccanthera*, Scrophulariaceae, wood anatomy.

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INTRODUCTION

*Penstemon* Mitch. is a large, complex, and predominantly herbaceous genus with its center of diversity in western North America. Within part of this area (the Californian Floristic Province and adjacent arid zones) suffrutescent to woody species of *Penstemon* are present in four of the five subgenera in the flora (Table 1). How is the wood of *Penstemon* constructed, how specialized is this wood, and to what extent does it present systematic or ecological patterns? Is wood of *Penstemon* distinct from that of the other six genera of woody Scrophulariaceae in the floristic province? Is woodiness polyphyletic in the family in this area, and if so, are the taxa convergent in some ecological feature? Questions such as these prompted this series of papers.

Subgeneric taxa of *Penstemon* (Table 1) are based on floral (especially anther) characters yet the range of floral syndromes indicates bees, butterflies, hummingbirds, and moths are important pollinators (Pennell 1935). Consequently, it is likely that the subgeneric taxa may not be natural (monophyletic) units as there is likely to be considerable floral convergence. Keck (1932) outlined the difficulties of establishing sectional alignment of one species treated here (*P. bridgesii*). Evidence from wood anatomy may help in understanding the relationships and evolution of character states in this complex genus.

Wood variation at and below the species level in *Penstemon* subgenus *Saccanthera* is the focus of this paper. Intersectional and intergeneric comparisons are deferred until data from the subgenera *Dasanthera* and *Penstemon* are presented (in preparation). Previous studies on the wood of *Penstemon* are too limited to address the questions posed above and earlier workers may have used a generic

definition that included taxa now segregated as *Keckiella* Straw. This literature is reviewed in Michener (1981).

An additional purpose of this series of papers is to provide an extensive and interpreted data-base on the wood of Scrophulariaceae for comparison with other taxa in the order. Studies attempting to understand familial definition and placement of small or poorly understood taxa such as *Halleria* L., *Leucophyllum* Humb. & Bonpl., or *Uncarina* (Baill.) Stapf (Outer and Veenendaal 1983) will be more convincing once wood comparisons for the Scrophulariaceae include more than the arboreal genus *Paulownia* Sieb. & Zucc.

#### MATERIALS AND METHODS

All samples were wild-collected and fixed in FAA by the author. I collected the largest and/or apparently oldest stem material I could find in a population in order to have "mature" wood, albeit many of the taxa are suffrutescent. Consequently, the samples are not of even age but the plants were sexually mature. Voucher specimens are deposited at RSA. The nomenclature above the species level presented in Table 1 follows Holmgren (1979); nomenclature at and below the species level presented in Table 2 follow Munz and Keck (1959), which differs from that of Holmgren (1984).

*Penstemon* woods are technically challenging to section due to the short internodal length, the small stem diameter, and the presence of unlignified rays as well as terminal bands of parenchyma (both of which promote section collapse). All material was softened in ethylene diamine (Carlquist 1982) prior to paraffin embedding and treated as described in Michener (1983). This procedure proved adequate but embedding in a rigid medium (resin) would have reduced internal

Table 1. Subgeneric Taxa of Californian *Penstemon*.

| Subgenus     | Section      | Subsection      | Number |
|--------------|--------------|-----------------|--------|
| Cryptostemon |              |                 | 0/1    |
| Dasanthera   |              |                 | 2/3    |
| Habroanthus  | Elmigera     |                 | 1/2    |
|              | Glabri       |                 | 0/1    |
| Penstemon    | Ambigui      | Ambigui         | 1/1    |
|              | Caespitosi   | Caespitosi      | 1/1    |
|              |              | Linarioides     | 1/1    |
|              | Cristati     |                 | 0/3    |
|              | Gentianoides | Centranthifolii | 1/3    |
|              | Spectabiles  |                 | 4/9    |
|              | Penstemon    | Arenarii        | 1/1    |
|              |              | Deusti          | 1/2    |
|              |              | Humiles         | 0/4    |
|              |              | Proceri         | 0/5    |
| Saccanthera  | Bridgesiani  |                 | 1/1    |
|              | Saccanthera  | Heterophylli    | 5/11   |

Generic definition of *Penstemon* follows Straw (1966); subgeneric treatment follows Keck (1951) with the redefinitions of Holmgren (1979). Species presence in the Californian flora and relevant synonymy follow Munz and Keck (1959), which differs from the nomenclature in Holmgren (1984). First number is the number of species collected for this study (0 = taxa not woody, but may be caespitose); second number is the number of species in the Californian flora.

Table 2. Wood features of *Penstemon* subgenus *Saccanthera*.

| Species                               | Collection     | 1  | 2        | 3       | 4   | 5   | 6        | 7        | 8  | 9    | 10   | 11 | 12 | 13 |
|---------------------------------------|----------------|----|----------|---------|-----|-----|----------|----------|----|------|------|----|----|----|
| <i>P. azureus</i> Benth.              |                |    |          |         |     |     |          |          |    |      |      |    |    |    |
| ssp. <i>angustissimus</i> (Gray) Keck | Michener 3776  | 5  | 176 ± 27 | 12 ± 6  | 2.6 | 208 | 235 ± 38 | 14 ± 2 b | 0  | 0.05 | 10.1 | —  | —  |    |
| ssp. <i>azureus</i>                   | Michener 4001  | 10 | 135 ± 29 | 14 ± 9  | 2.5 | 268 | 183 ± 21 | 12 ± 2 d | 19 | 0.05 | 7.0  | +  | —  |    |
|                                       | Michener 4008  | 3  | 131 ± 28 | 14 ± 8  | 2.6 | 196 | 186 ± 26 | 14 ± 3 c | 16 | 0.07 | 9.3  | —  | —  |    |
|                                       | Michener 4010a | 8  | 119 ± 28 | 20 ± 10 | 3.2 | 225 | 195 ± 39 | 15 ± 2 d | 27 | 0.08 | 10.5 | +  | —  |    |
| <i>P. bridgesii</i> Gray              | Michener 3993  | 7  | 129 ± 21 | 24 ± 20 | 3.0 | 228 | 183 ± 32 | 16 ± 2 d | 6  | 0.10 | 13.5 | —  | —  |    |
|                                       | Michener 3999  | 4  | 145 ± 22 | 14 ± 9  | 2.9 | 233 | 178 ± 40 | 13 ± 1 c | 14 | 0.06 | 8.7  | —  | —  |    |
|                                       | Michener 4006  | 4  | 124 ± 24 | 19 ± 13 | 3.5 | 191 | 169 ± 39 | 12 ± 1 d | 23 | 0.09 | 12.3 | +  | —  |    |
|                                       | Michener 4023  | 4  | 112 ± 25 | 19 ± 12 | 2.8 | 212 | 186 ± 38 | 18 ± 2 b | 8  | 0.08 | 10.0 | —  | +  |    |
|                                       | Michener 4064  | 6  | 122 ± 28 | 17 ± 11 | 3.2 | 139 | 193 ± 34 | 12 ± 1 c | 15 | 0.12 | 14.9 | —  | —  |    |
| <i>P. caesius</i> Gray                | Michener 4027  | 16 | 92 ± 24  | 12 ± 9  | 2.7 | 332 | 129 ± 28 | 13 ± 3 a | 0  | 0.03 | 3.3  | —  | —  |    |
| <i>P. heterophyllus</i> Lindl.        |                |    |          |         |     |     |          |          |    |      |      |    |    |    |
| ssp. <i>australis</i> (M. & J.) Keck  | Michener 3972  | 2  | 117 ± 20 | 18 ± 26 | 2.2 | 171 | 204 ± 41 | 16 ± 2 a | 0  | 0.10 | 12.3 | —  | +  |    |
|                                       | Michener 4083  | 8  | 109 ± 16 | 15 ± 9  | 2.6 | 239 | 198 ± 30 | 15 ± 2 b | 2  | 0.62 | 6.8  | —  | +  |    |
| ssp. <i>heterophyllus</i>             | Michener 4065  | 5  | 114 ± 16 | 20 ± 10 | 2.6 | 218 | 184 ± 25 | 15 ± 3 c | 3  | 0.09 | 10.4 | —  | +  |    |
|                                       | Michener 4076  | 4  | 116 ± 26 | 22 ± 11 | 2.2 | 144 | 205 ± 36 | 18 ± 3 a | 0  | 0.15 | 17.7 | —  | —  |    |
| <i>P. laetus</i> Gray                 |                |    |          |         |     |     |          |          |    |      |      |    |    |    |
| ssp. <i>laetus</i>                    | Michener 3967  | 4  | 128 ± 23 | 14 ± 8  | 2.4 | 211 | 187 ± 32 | 12 ± 2 b | 0  | 0.06 | 8.4  | +  | —  |    |
|                                       | Michener 4147  | 4  | 100 ± 24 | 12 ± 11 | 2.4 | 354 | 160 ± 30 | 13 ± 2 b | 15 | 0.03 | 3.3  | +  | —  |    |
| ssp. <i>roezlii</i> (Regel) Keck      | Michener 4016a | 5  | 120 ± 28 | 11 ± 9  | 3.0 | 261 | 172 ± 28 | 16 ± 2 b | 8  | 0.04 | 5.0  | —  | —  |    |
| <i>P. scapoides</i> Keck              | Michener 3996  | 10 | 98 ± 14  | 10 ± 9  | 3.1 | 300 | 148 ± 33 | 14 ± 2 b | 0  | 0.03 | 3.2  | —  | —  |    |

Key to columns: 1, number of growth rings (presumably age in years).—2, Vessel element length,  $\mu\text{m}$ .—3, Vessel element diameter (internal),  $\mu\text{m}$ .—4, Vessel wall thickness.—5, Number of vessels per mm.—6, Fiber-tracheid length,  $\mu\text{m}$ .—7, Fiber-tracheid diameter.—8, Maximal ray development (a = absent, b = present but not massive, c = massive, d = massive but ray cells irregularly lignified).—9, Per cent ray tissue by proportional area.—10, Vulnerability ratio (Col. 2 divided by Col. 5).—11, Mesomorphy ratio (Col. 10 multiplied by Col. 1).—12, Presence of scalariform perforation plates.—13, Presence of crystals. (Columns 2, 3, 6 and 7 are mean and standard deviation; for sample sizes, see methods.)

tearing and improved the photographic quality of many sections. Measurement methods follow my previous work on Californian Scrophulariaceae (Michener 1981, 1983) with the following clarifications and elaborations. Vessel element length for the average values (Table 2) is measured from macerations. Care was taken when preparing the macerations to obtain (with few exceptions) the last year's growth. Only those cells parallel with a preset eyepiece micrometer are measured ( $n = 25$ ). This insures much of a slide is scanned and avoids one sampling bias (vessel element distribution by length is not necessarily random within a maceration). Vessel element length for the age-on-length data (Fig. 13) is gathered from radial sections from one or several adjacent vessels for each year specified. This accounts for the small sample size ( $n = 10$ ) and the minor inconsistencies between the two methods of measuring cell length: values from radial sections are well known to deviate from "true" values as the entire cell may not be in the plane of the section. Vessel element diameter (internal) was calculated by measuring the diameter of all of the elements present in an arc of a transection of the last growth cycle. Since all the cells in an area were measured, sample size ranges from  $n = 25$  to  $n = 50$  (except for *P. azureus* [4008] and *P. bridgesii* [4064];  $n = 23$ ). Wall thickness is based on a sample size of  $n = 10$ . The value of vessels per square millimeter was calculated from the final growth ring. Where this growth ring was incomplete additional measurements were taken from the preceding year's growth. Ten half-fields were scored according to two schemes. If the ring width was less than a full field, half the counts began at the beginning of the ring; the other half were reversed and began at the end of the ring. If the growth ring was wider than one field, the ring was sampled from successive but laterally displaced bands. Ray tissue proved to be notably variable as a proportion of the cross-sectional area of certain stems. All stems were surveyed to record the maximal development of ray tissue, but only a single, arbitrarily chosen sector was photographed for proportional weighing. Photographs were taken at a uniform magnification and the prints developed as one lot. The prints were air dried for over one week and subsectioned by tissue type for proportional weighing.

## RESULTS

Table 2 summarizes over 2700 cell measurements for wood of *Penstemon* subgenus *Saccanthera*. Values for internal vessel element diameter (Column 3) are conspicuous for their large standard deviations caused by departures from normality (see below).

Vessel elements are short and narrow by the criteria of Metcalfe and Chalk (1950). Average vessel element length ranges from a low value of  $92\ \mu\text{m}$  (*P. caesius*) to a high value of only  $176\ \mu\text{m}$  (*P. azureus*). Vessel element length (reflecting cambial-initial length) consistently decreases with age or fluctuates in a statistically insignificant manner after an initial decrease (Fig. 13). Average vessel element diameter is quite narrow, ranging from a low value of  $10.9\ \mu\text{m}$  (*P. scapoides*) to a high value of only  $24.5\ \mu\text{m}$  (*P. bridgesii*). The standard deviation of vessel element diameter equals or exceeds 50% of the mean value in all cases, with notably broad ranges in *P. bridgesii* (3993), *P. heterophyllus* (3972), *P. laetus* (4016a, 4147), and *P. scapoides* (3996). The underlying phenomenon is the presence of terminal bands of very narrow vessels (Fig. 1, 3, 5). These narrow vessels cause a varyingly skewed (sometimes eccentrically bimodal) distribution of vessel

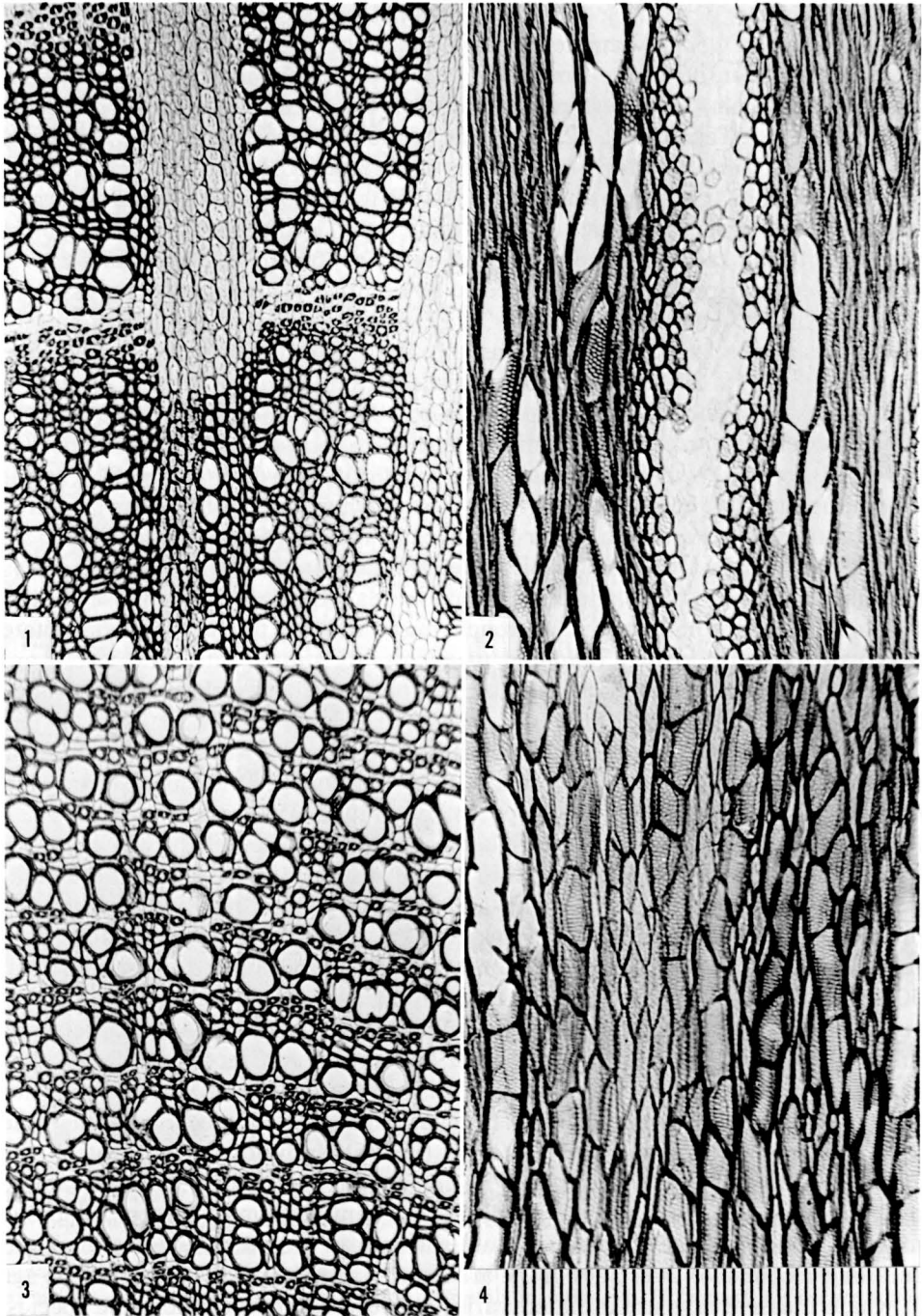


Fig. 1–4. Wood sections of *Penstemon bridgesii* and *P. caesius*.—1. *P. bridgesii* (Michener 3999). Transection: narrow vessels (arrows) in terminal band are intermixed with axial parenchyma. Ray lignification incomplete.—2. *P. bridgesii* (Michener 4006). Tangential section: multicellular ray massive, lignification of ray cells erratic; uniseriate ray right of center.—3, 4. *P. caesius* (Michener 4027).—3. Transection: narrow vessels (arrows) often single-file in terminal band followed by axial parenchyma.—4. Tangential section: cambium locally storied. (Fig. 1–4, magnification scale below Fig. 4. Divisions = 10  $\mu\text{m}$ .)



element diameter depending on the proportional width of the terminal band. The average value of vessel diameter is used in the vulnerability and mesomorphy ratios. Perforation plates are simple with rare exceptions (notably in the primary xylem) where scalariform perforation plates have one, two, forked, or incomplete bars (Fig. 11, 12; Table 2, col. 12). Vascular tracheids (imperforate vessel elements) are rare; they were noted in macerations of *P. azureus* (4001) and *P. bridgesii* (4023); judged by their narrowness they must be from the terminal band of narrow vessels. Vessel grouping proved difficult to quantify. Solitary and small groups of vessels (often in radial rows) occur in all samples, but in the terminal band of vessels occur groups in excess of 50 cells. By contrast, wide earlywood vessels of *P. caesius* are laterally grouped (Fig. 3). Tertiary helical thickenings are present in the vessels of all samples, but are usually restricted to the narrow vessels (Fig. 7). Vessel pitting is of alternate, circular bordered pits, although the tertiary helical thickenings may cause some of the pits to be elliptical in outline.

Fiber-tracheids form the mechanical tissue and average 1.2 (*P. bridgesii* [3999]) to 1.8 (*P. heterophyllus* [4083]) times the length of the vessel elements. The pit margins range from notably broad (Fig. 8) to quite narrow (Fig. 9). Fiber-tracheids of *P. caesius* (4027) are notable for their lack of thick secondary walls (Fig. 3, 4).

Axial parenchyma consists of biseriate strands (Fig. 7). Axial parenchyma is both paratracheal (scanty) and in terminal bands with the narrow vessels (Figs. 1, 3, 5, 7). In addition to the axial parenchyma strands are thin-walled, nonseptate cells with broad, narrowly bordered to apparently simple pits. These cells are intermediate between parenchyma and thin-walled fiber-tracheids with pits as broad as those in Figure 8.

Ray parenchyma is enormously variable within and between species. Notable variation occurs in presence or absence of rays, the age at which massive rays are initiated, and the extent of development of a notable secondary wall (Fig. 2). Pitting of the ray cells that have developed secondary walls is slightly to distinctly bordered whether the adjacent cell is a ray or vessel. Multiseriate rays are composed of erect, square, procumbent, and irregular cells. Erect and square cells predominate at the margins of the rays; broad rays thus have relatively numerous procumbent cells in the center (Fig. 2). Massive heterocellular rays (greater than 50 cells tall and five cells wide) are found in *P. azureus*, *P. bridgesii* (Fig. 2, 3), and *P. heterophyllus*; these rays are prominent in tangential view in unsectioned material. Cells of the massive rays often lack prominent secondary walls in *P. azureus* and *P. bridgesii* (Fig. 2)—no consistent pattern in wall lignification has been noted. Presence of raylike areas (but such areas not counted as rays in Table 2) is evident in *P. caesius* and *P. laetus* (Fig. 6). Individuals (but not all the samples) of two species (*P. caesius*, *P. heterophyllus*) are rayless and one sample of *P. azureus* (3776) has but one small ray. A quantification of percent ray tissue in cross-sectional view (Table 2, Col. 9) shows rays are quite variable in extent and may account for over 20% of the area in *P. azureus* and *P. bridgesii*. The age at which massive rays are initiated varies between samples of the same species. In *P. azureus*, sample 4001 has large rays by year three, but most such rays are not initiated until year seven. By contrast, in sample 4064 such rays are numerous by year two.

Growth rings are distinct in all samples (Fig. 1, 3, 5) and most correspond most closely to Type XI of Carlquist (1980); the widest vessels are formed after the

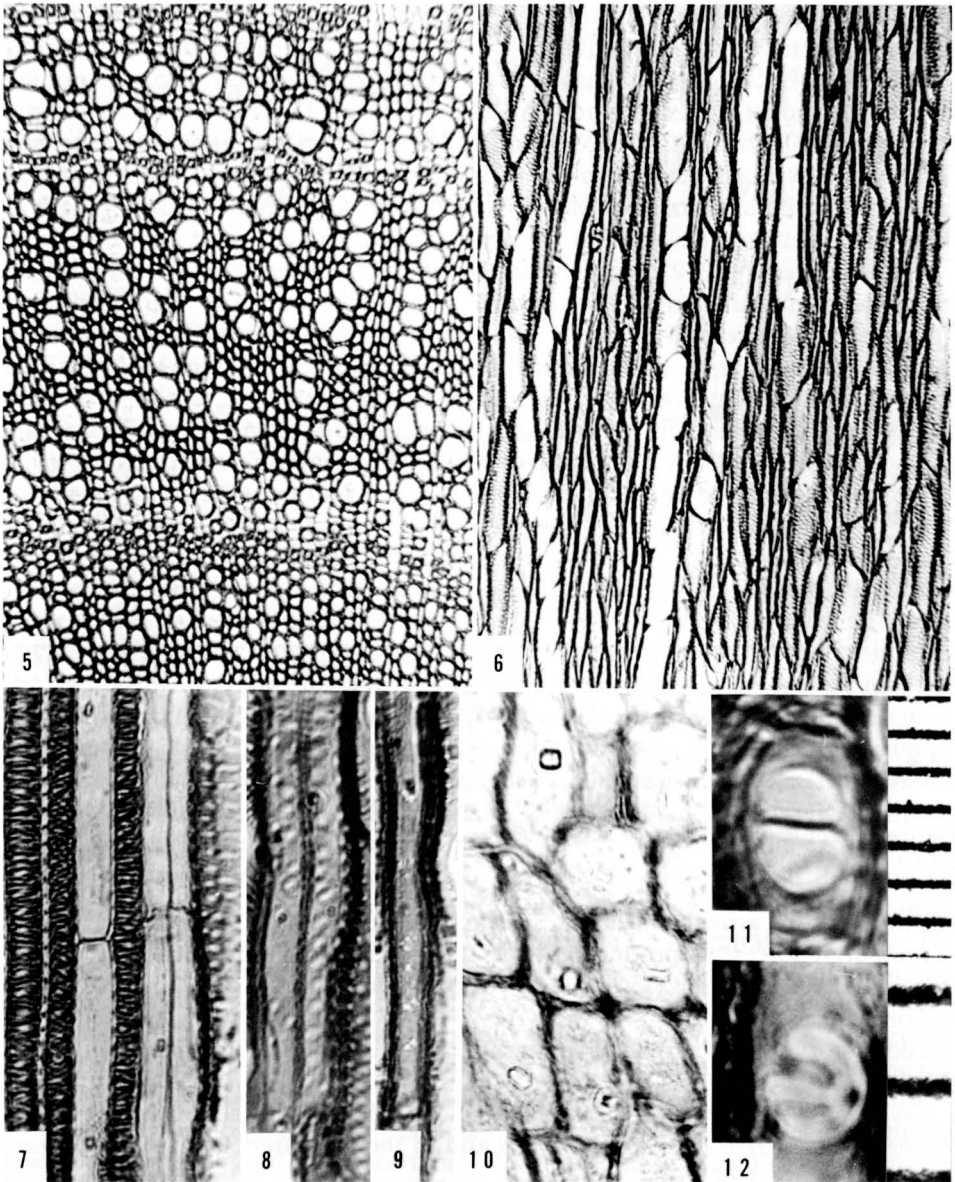


Fig. 5-12. Wood features of *Penstemon*.—5, 6. *P. laetus* (Michener 4147).—5. Transection; rays absent but breaks (arrows) in terminal band just internal to the cambium are likely sites of multicellular ray initiation.—6. Tangential section: raylike areas highlighted by arrows. Cells tending to storied orientation upper center and left.—7, 9. *P. azureus* (Michener 4001). Details of cell types.—7. Biseriate strand of axial parenchyma and narrow vessels in terminal band.—8, 9. Range of pitting on fiber-tracheids.—10. *P. bridgesii* (Michener 3999). Crystals in pith.—11. *P. bridgesii* (Michener 4006). Scalariform perforation plate with one bar.—12. *P. laetus* (Michener 3967). Perforation plate with two incomplete bars. (Fig. 5, 6, magnification scale below Fig. 4; Fig. 7-10, magnification scale by Fig. 11; Fig. 11, 12, magnification scale by Fig. 12. Divisions = 10  $\mu$ m).



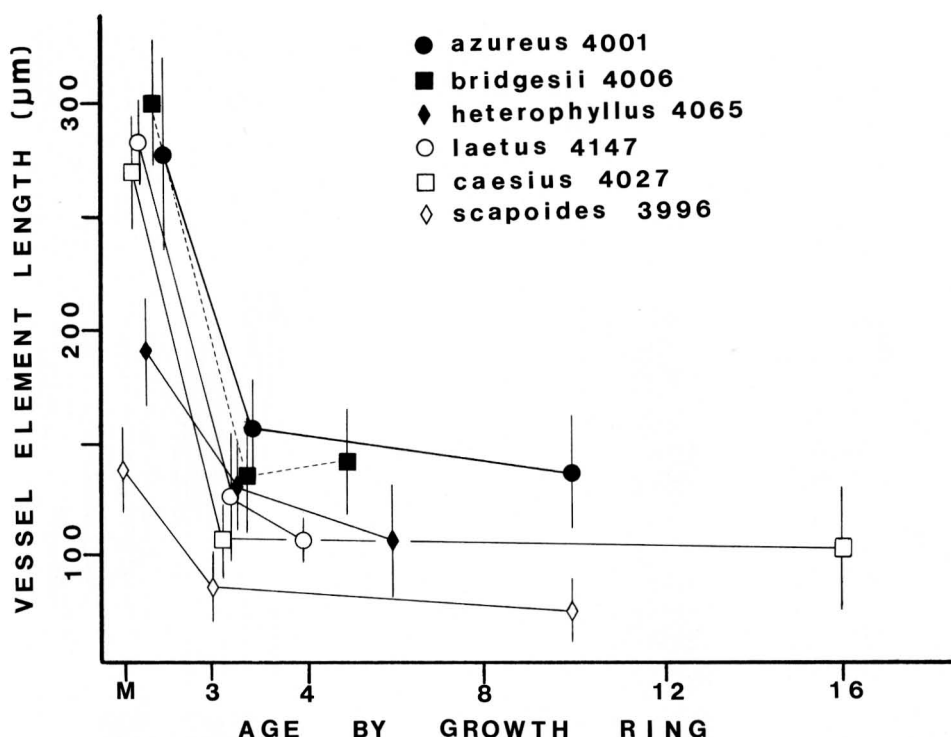


Fig. 13. Vessel element length by age. Scale on age axis breaks between rings 3 and 4. M = metaxylem of first year. Bars = standard deviation ( $n = 10$  for rings 3 to 16,  $n = 3$  to 10 for metaxylem). Symbols for M and ring 3 are staggered to reduce overlap. The increase in vessel element length for the final year of *P. bridgesii* (dotted line) is statistically insignificant in comparison with ring 3 ( $P < 0.10$ ,  $t = 0.6547$ , 18 d.f.).

beginning of the growth ring and a seasonal (terminal) band of axial parenchyma is present. The vessels produced at the end of the season are extremely narrow (Fig. 1, 3, 5); a lateral view (Fig. 7) demonstrates that these cells are indeed perforate.

Local storying of cambia is noticeable in *P. caesius* (Fig. 4) and *P. laetus* (Fig. 6).

Crystals (rods, prisms, druses) are found in the pith of some samples of *P. bridgesii* (Fig. 10) and *P. heterophyllus* and in the ray parenchyma of *P. azureus* (3776) (Table 2, Col. 13).

#### DISCUSSION

Wood of *Penstemon* subgenus *Saccanthera* is highly specialized in four features, and a paedomorphic origin of the wood (Carlquist 1962) accounts for the juxtaposition of several characteristics. The paedomorphic characteristics are: the decrease in vessel element length (reflecting the length of cambial initials) without a subsequent increase in length as the cambium ages; the presence of occasional scalariform perforation plates outside of the primary stem tissue; and the tendency to or attainment of raylessness. Advanced features of the vessel elements include the simple perforations (other than the rare scalariform perforation plates noted

above), the alternate circular bordered pits, and the short element length. The presence of cells intermediate between parenchyma cells and fibers is a specialization also known from other advanced dicot genera (Carlquist 1958; Welle and Koek-Noorman 1978). The notable specialization of the rays is the reduction or loss of ray tissue in several samples. Carlquist's (1975) functional interpretation is that this loss of rays (caused by lack of transverse divisions, or "suppression" of the ray initials—Barghoorn [1941]) increases the mechanical ability of the plant. The loss of ray tissue by arrested development (nondivision or delayed division of the initials) is an example of heterochrony (Gould 1977). What is striking is that the timing or extent of initiation of massive heterocellular rays is not yet fixed within species: in *P. bridgesii* some of the older specimens finally differentiate additional ray material with age. The final specialization is the presence of locally storied cambia in two of the species. Bailey (1923) demonstrated that storying is a specialization in higher dicots. Cumbie and Mertz (1962) showed that the conspicuousness of storying varies in relation to plant habit within the genus *Sophora* L. but they were unaware that any pedomorphic phenomena might be confounding their interpretation.

The samples presented in Table 2 and Figures 1–6 indicate that woods of *Penstemon* subgenus *Saccanthera* are highly stereotyped for vessel and growth ring characteristics, but are highly variable for ray and some fiber-tracheid/parenchyma characteristics. Interpreting the data of Table 2 is best done by considering the significance and the interaction of four major parameters: taxonomic identity; sample age; the vessel characters underlying the ecological indices (vulnerability and mesomorphy); and the provenance of the samples. A view of the data by taxon shows that most of the variation in ray characteristics (including presence or absence) is infraspecific. Since my sampling method did not address population-level variation (it was not anticipated to be significant), the extent of this variation remains unknown. For the multisample species it is clear that rays are least developed in *P. laetus*. Completely rayless individuals are found in *P. caesius* and *P. heterophyllus*. Age is a confounding variable in interpreting Table 2. The clustering of over half the samples in years four to six and the spread of remaining points vitiates most correlations. All the wood samples are from "mature" plants in the sense that every plant was sexually mature. Three samples (*P. azureus* [4001], *P. caesius* [4027], and *P. scapoides* [3996]) are notably older than the rest and merit discussion in relation to mesomorphy and source. Two of these samples, *P. caesius* and *P. scapoides*, have both the shortest vessel element lengths and the lowest mesomorphy ratios in the table. Both samples are from open coniferous forests bordering the Mojave and Great Basin deserts (*P. scapoides* is a restricted endemic of a desert mountain range), suggesting that the vessel element parameters underlying low mesomorphy values are linked with survivorship in drought-stressed habitats. This view is supported by the mesomorphy value of the only sample of *P. bridgesii* collected from a desert mountain range. *Penstemon bridgesii* 3999 was collected several kilometers from the site of *P. scapoides*; it has the lowest mesomorphy value for the species. Further consideration of correlated provenance and wood features is deferred until data from the remaining two sections are presented as seven sites of sympatric collections (17 samples) are involved.

An interpretation of the ecological significance of vessels with wide pits in

parenchyma bands was advanced by Carlquist and Eckhart (1984). They noted this phenomenon in several unrelated taxa (including *P. bridgesii*) from the Californian flora and suggested that it is of benefit during the renewal of water transport after the seasonal drought. The other species of subgenus *Saccanthera* show such vessels in the terminal bands of axial parenchyma. In light of the work of Braun (1983) showing that axial parenchyma and "parenchymatous contact cells of the xylem rays" influence water uptake by leafless temperate trees, it is likely that the unlignified ray cells also may be actively involved in the storage or regulation of osmotically active substances needed for the resumption of growth following the dry season.

The evolutionary shift to a secondarily woody or suffrutescent habit in *Penstemon* subgenus *Saccanthera* is demonstrated by the paedomorphic features. The variation in ray characteristics within species indicates that the genetic regulation of wood development is yet unfixed, perhaps even at the populational level. This poor developmental regulation of part of the wood structure suggests that the variation is: 1) a recent novelty; 2) not selectively disadvantageous; or 3) maintained by some mechanism, such as hybridization. Regardless of the evolutionary time frame for this shift in habit, *Penstemon* species that are woody (and are therefore long-lived) should have, in relation to the herbaceous species, reproductive and life history characteristics closer to "K" than "r" selected taxa (Gould 1977; but see Boyce, 1984, for restriction of concepts and terminology). The ecological information from such studies would provide a strong base for placing secondary woodiness in an evolutionary context in the genus. Finally, the wood architecture of *Penstemon* subgenus *Saccanthera* seems to limit the taxa to plants of only minor stature, even as shrubs. The short fiber-tracheids and the presence of terminal bands of axial parenchyma (as well as the poorly lignified rays) lead to a brittle and mechanically weak wood, thus indicating genetic limits to the structural habits that can be presented to natural selection.

#### ACKNOWLEDGMENTS

I thank S. Carlquist, Noel Holmgren, and Karl Vincent for their comments as reviewers.

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